

## First Hominoid From the Miocene of Ethiopia and the Evolution of the Catarrhine Elbow

BRIAN G. RICHMOND,<sup>1\*</sup> JOHN G. FLEAGLE,<sup>2</sup> JOHN KAPPELMAN,<sup>3</sup>  
AND CARL C. SWISHER III<sup>4</sup>

<sup>1</sup>Smithsonian Institution, Washington, DC 20560

<sup>2</sup>Department of Anatomical Sciences, School of Medicine, State University of New York at Stony Brook, Stony Brook, New York 11794

<sup>3</sup>Department of Anthropology, University of Texas at Austin, Austin, Texas 78712-1086

<sup>4</sup>Berkeley Geochronology Center, Berkeley, California 94709

**KEY WORDS** fossil apes; anthropoids; postcranium; forelimb; *Turkanapithecus*; *Pliopithecus*; multivariate analysis

**ABSTRACT** The first known fossil ape from the early-middle Miocene of Fejej, Ethiopia, is described here. The specimen, FJ-18SB-68, is a partial ulna from a locality dated by <sup>40</sup>Ar/<sup>39</sup>Ar and paleomagnetic methods to a minimum age of 16.18 MYA. Compared to a variety of extant and fossil ulnae, FJ-18SB-68 is most similar to *Turkanapithecus*, *Proconsul*, and *Pliopithecus*, and appears to have been an arboreal quadruped with substantial forearm rotational mobility.

Among the extant ulnae, canonical variates analysis successfully discriminates platyrrhines from catarrhines and within the latter, cercopithecoids from hominoids. Basal catarrhines (e.g., *Aegyptopithecus*) are platyrrhine-like in their morphology. Two basic trends appear to evolve from this generalized template: one with less mobile and more habitually pronated forearms, as seen in living and fossil cercopithecoids (including *Victoriapithecus* and *Paracolobus*), and another with greater forearm rotational mobility in fossil and modern hominoids. Primitive Miocene apes, including *Proconsul*, *Turkanapithecus*, and FJ-18SB-68, share with extant hominoids a more laterally positioned and laterally facing radial notch and an incipient trochlear keel. This morphology, along with a large insertion area for *m. brachialis*, suggests a departure from the more habitually pronated hand posture of monkeys and may indicate greater climbing abilities in these arboreally quadrupedal apes. Later Miocene apes, such as *Oreopithecus* and *Dryopithecus* share additional morphological features with hominoids, indicating considerable suspensory and climbing capabilities. *Am J Phys Anthropol* 105:257-277, 1998. © 1998 Wiley-Liss, Inc.

The elbow joint of living apes and humans is one of our most distinctive anatomical regions. The unique features of the hominoid elbow are thought to be related to extensive abilities of pronation and supination pertaining to suspensory locomotor adaptations (e.g., Jenkins, 1973; Rose, 1988). Analysis of this region has long played an important role in understanding the locomotor adaptations and phylogenetic relationships of fossil apes (e.g., Napier and Davis, 1959; Fleagle et al., 1975;

Fleagle, 1983; Rose, 1988, 1993; Larson, 1993).

In this article, we describe a partial ulna of a fossil ape from the early-middle Miocene

Contract grant sponsor: National Geographic Society; contract grant numbers 4393-90, 4600-91; Contract grant sponsor: NSF; contract grant number SBR-9319193; Contract grant sponsors: L.S.B. Leakey Foundation, The Wenner-Gren Foundation.

\*Correspondence to: Brian G. Richmond, Human Origins Program, Department of Anthropology, MRC 112, Smithsonian Institution, Washington, DC 20560.  
E-mail: Richmond.Brian@NMNH.SI.EDU

Received 29 May 1997; accepted 31 October 1997.

TABLE 1. Laser incremental-heating  $^{40}\text{Ar}/^{39}\text{Ar}$  data

Step	% $^{39}\text{Ar}$	$^{40}\text{Ar}/^{39}\text{Ar}$	$^{37}\text{Ar}/^{39}\text{Ar}$	$^{36}\text{Ar}/^{39}\text{Ar}$	$^{40}\text{Ar}^*/^{39}\text{Ar}$	% $^{40}\text{Ar}^*$	Age	SD
<i>Sample F21/7368-01</i>								
A	0.9	44.237	4.162	0.1298	6.240	14.1	15.68	1.68
B	4.7	15.472	3.322	0.0304	6.782	43.7	17.03	0.30
C	8.7	10.480	2.757	0.0141	6.539	62.3	16.43	0.16
D	14.3	8.297	2.377	0.0069	6.466	77.8	16.24	0.08
E	20.9	7.457	2.102	0.0041	6.427	86.1	16.14	0.07
F	24.9	6.823	1.985	0.0019	6.443	94.3	16.19	0.07
G	8.8	6.698	3.760	0.0022	6.364	94.8	15.99	0.12
H	12.3	6.728	5.992	0.0028	6.426	95.1	16.14	0.11
I	4.5	6.703	6.016	0.0025	6.467	96.1	16.25	0.14

of Fejej, Ethiopia (Asfaw et al., 1991; Bown et al., 1994). The limited Miocene deposits in this area have yielded a rich flora of fossil fruits and seeds (Tiffney et al., 1994), as well as numerous remains of large terrestrial mammals (Fleagle et al., 1994). However, the ulna is the first Miocene ape known from Ethiopia. In describing the fossil ape ulna, we compare it with other fossil apes from both Africa and Europe, as well as extant anthropoids. Multivariate methods are employed to identify the features of the proximal ulna which discriminate taxonomic groups. These comparisons provide a broad evolutionary context for examining the adaptive and phylogenetic evolution of the elbow joint in catarrhine evolution.

#### LOCALITY AND GEOCHRONOLOGY

The Miocene locality of FJ-18 lies on the Fejej Plain of western and southernmost Ethiopia (Tiffney et al., 1994). The fossils at locality FJ-18 include diverse plant and animal remains from two distinct levels (Tiffney et al., 1994). Mammal fossils occur in the upper level and are found within an intraclastic conglomerate that consists of subangular to well-rounded granules in a gray volcanic mudstone. The conglomerate ranges from clast to matrix-supported and fills a minor paleovalley. The conglomerate is capped by a fine-grained porphyritic plagioclase and pyroxene-rich theoleiitic lava. This lava was sampled for radioisotopic dating, with samples trimmed on the outcrop. The basalt has a well-defined plateau and provides a  $^{40}\text{Ar}/^{39}\text{Ar}$  age of  $16.18 \pm 0.05$  MYA (Table 1 and Fig. 1). Other volcanic lavas underlying the fossil horizon were found to be too altered to permit dating.

The capping basalt was also sampled for paleomagnetic analysis. Step-wise thermal demagnetization (Fig. 2) shows a steep decrease in intensity to  $500^\circ\text{C}$  and random directions above  $575^\circ\text{C}$ . Vectors for each sample ( $n = 3$ ) were calculated with principal component analysis (Kirschvink, 1980) and reveal that the basalt is reversely magnetized (virtual geomagnetic pole latitude =  $-45^\circ$ ). The steep positive inclination is unusual for a site that lies this close to the equator and suggests that the remanent magnetism may have been locked in near a polarity transition. The time scale of Cande and Kent (1995) places the date of  $16.18 \pm 0.05$  MYA solidly within the normal interval of chron C5Cn.1n, while other time scales (e.g., Berggren et al., 1985) place this date near the older end of the long reversely magnetized interval of C5Br. The reversed polarity and positive inclination of this basalt tentatively suggests that it could lie near the upper (or even lower) boundary of C5Cn.1n but the results from this single site are insufficient to attempt to better resolve the timing of this polarity transition.

These data provide a minimum age of 16.18 MYA for locality FJ-18 and add the Fejej region to the growing number of Miocene fossil localities in Ethiopia (Suwa et al., 1991, and references therein; Wolde-Gabriel et al., 1991). This age falls within the range of K-Ar ages reported for volcanics from Buluk ( $15.7 \pm 0.2 - 17.2 \pm 0.2$  MYA) located to the southeast just across the border in Kenya that also cap fossiliferous primate-bearing sediments (McDougall and Watkins, 1985; Leakey and Walker, 1985; Watkins, 1989). Although both FJ-18 and

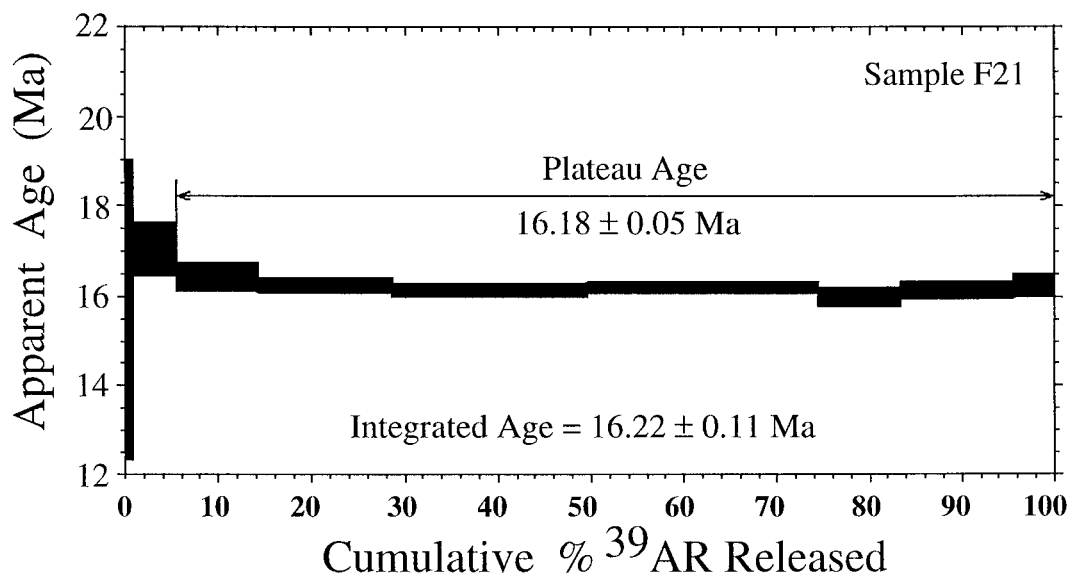


Fig. 1. Plateau and integrated ages for the basalt that caps locality FJ-18 dated by the laser incremental-heating  $^{40}\text{Ar}/^{39}\text{Ar}$  method. The basalt sample was shielded during irradiation with a thin layer of cadmium to minimize the production of interference isotopes. For sample F21:  $J$  (Irrad. #102B) =  $0.0013988 \pm 0.0000013$ .  $J$  was determined from replicate single crystal analyses of the co-irradiated monitor mineral, Fish Canyon sanidine with an age of 27.84 Ma. Correction factors:  $(^{39}\text{Ar}/^{37}\text{Ar})\text{Ca} = 6.85 \pm 0.24 \times 10^{-4}$ ;  $(^{36}\text{Ar}/^{37}\text{Ar})\text{Ca} = 2.74 \pm 0.05 \times 10^{-4}$ ;  $(^{40}\text{Ar}/^{39}\text{Ar})\text{K} = 9.0 \pm 3 \times 10^{-4}$ ;  $^{40}\text{Ar}/^{36}\text{Ar}$  discrimination =  $1.083 \pm 0.003$ . Decay constants are those recommended by Steiger and Jäger (1977). The analytical procedures employed follow those described in Swisher et al. (1994) and references therein. Incremental heating of the basalt and total fusion of single crystals of the monitor mineral were accomplished with a 6W Coherent Ar-ion laser. The basalt sample was

incrementally heated by step-wise increasing output from the laser with a defocused laser beam for 45 sec to heat evenly the 2-mm diameter sample wells. Released gases were purified by two SAES C-50 getters operated at approximately 4,000°C. Argon was measured in an on-line Mass Analyzer Product 215 noble-gas mass spectrometer operated in the static mode, using automated data collection techniques. Laser heating, gas purification, and mass spectrometry were completely automated following computer programmed schedules. The uncertainties associated with the individual incremental apparent ages are 2s errors, while the plateau ages are calculated as the weighted (by inverse variances) mean of all increments defining the plateau and the uncertainties that accompany the plateau ages are standard errors (SE). Plateau definition basically follows Fleck et al. (1977). Data are provided in Table 1.

Buluk have only capping ages, both sites share a number of plant and mammal taxa which adds support to the idea that these two sites are roughly contemporaneous (Tiffney et al., 1994).

#### MATERIALS AND METHODS

A comparative sample of extant anthropoids was chosen to represent a wide range of locomotor adaptations and taxonomic groups: *Alouatta seniculus* ( $n = 30$ ), *Ateles sp.* ( $n = 11$ ), *Gorilla gorilla* ( $n = 5$ ), *Hylobates agilis* ( $n = 4$ ), *Macaca fascicularis* ( $n = 6$ ), *Macaca nemestrina* ( $n = 7$ ), *Pan troglodytes* ( $n = 22$ ), *Papio hamadryas* ( $n = 24$ ), *Presbytis melalophus* ( $n = 4$ ), and *Presbytis obscura* ( $n = 6$ ). The extant sample is from skeletal collections housed at the Mammal-

ogy Departments of the American Museum of Natural History and Smithsonian's National Museum of Natural History. Fossil ulnae were chosen to include taxa, particularly those from the Miocene of Africa, that provide a broad evolutionary context from which to examine the evolution of the elbow in catarrhines (Table 2). Measurements were taken on casts, but the original fossils of many specimens (e.g., FJ-18SB-68, KNM-WT 16950R, YPM 23940) were inspected by J.G.F.

Measurements included in this analysis were selected to capture size and shape information of the proximal ulna that may be related to joint posture and movement (Table 3, Fig. 3). Several of these measures were adapted from Begun (1992a). In order

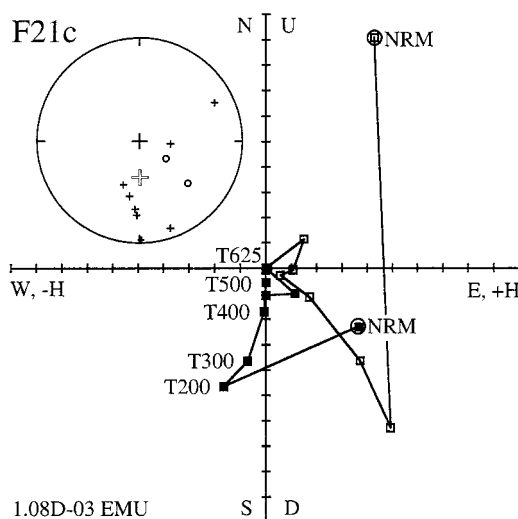


Fig. 2. Results from demagnetization treatments of the dated basalt that caps FJ-18. Sample F21c is characteristic of the other samples from the basalt and demonstrates a stable reversed declination and positive inclination from 200°–500°C and random directions above 575°C. The basalt is reversely magnetized. Symbols: solid squares equal declination, hollow squares equal inclination, crosses are lower hemisphere, hollow circles are upper hemisphere, hollow cross is the mean of the three samples (declination equals 183.0°, inclination equals 59.6°,  $R$  equals 2.97) calculated with Fisher statistics (Fisher, 1953). Samples were measured with a 2G SCT superconducting magnetometer in a magnetically shielded room at the University of Texas at Austin. Step-wise thermal demagnetization was conducted with a Schonstedt Thermal Demagnetizer (TSD-1).

to measure the angle of the radial notch, the ulna was placed horizontally in a padded vicegrip with the sigmoid notch and coronoid process facing superiorly. For most extant samples, the humerus was positioned vertically on the superiorly directed sigmoid notch in order to help orient the ulna. With the ulna firmly in position, one arm of a goniometer was placed flush against the center of the radial notch in a transverse plane. The other arm fell vertically under the influence of gravity, and the angle of the radial notch was recorded. Angles are difficult to measure, in this case primarily due to the reliance on accurate, consistent orientation of the ulna. To test the reliability of this measurement, an *Alouatta* ulna (conservatively chosen for its small radial notch) was positioned and measured ten times over a two-month period and all measures fell within four degrees of each other (mean = 45.5, s.d. = 1.18, range: 43–47).

Statistical analyses were performed on both raw and size-adjusted shape data. The size of the ulna is taken as the geometric mean (GM) of the subset of measurements that capture the width, depth, and length of the proximal ulna, calculated as the  $n$ th root of the product of  $n$  measurements (Mosimann, 1970; Darroch and Mosimann, 1985;

TABLE 2. Fossil primate ulnae included in this analysis

Specimen	Locality	Age (MYA)	Reference	Taxon
FJ-18SB-68	Fejej, Ethiopia	>16.18	this manuscript	indet.
KNM-WK16950R	Kalodirr, Kenya	16–18	Leakey et al., 1988	<i>Turkanapithecus kalakolensis</i>
KNM-RU2036	Rusinga Island, Kenya	e. Miocene	Walker & Pickford, 1983	<i>Proconsul heseloni</i>
KNM-RU1786	Rusinga Island, Kenya	e. Miocene	Szalay & Delson, 1979	<i>Proconsul nyanzae</i>
KNM-RU2099E	Rusinga Island, Kenya	e. Miocene	LeGros Clark & Thomas, 1951	<i>Dendropithecus macinnesi</i>
KNM-FT3381	Fort Ternan, Kenya	13–14	Andrews & Walker, 1976	hominoid?
KNM-BC3D	Lake Baringo, Kenya	m. Pliocene	Birchette, 1982	<i>Paracolobus chemeroni</i>
KNM-MB32	Maboko Island, Kenya	15–16	von Koenigswald, 1969	<i>Victoriapithecus macinnesi</i>
YPM23940	Fayum, Egypt	>33	Fleagle et al., 1975	<i>Aegyptopithecus zeuxis</i>
RUD22	Rudabanya, Hungary	11	Kretzoi, 1975; Morbeck, 1983	<i>Dryopithecus branconi</i>
Klein Hadersdorf	Klein Hadersdorf, Austria	13–14	Ehrensberg, 1938; Begun, 1992a	<i>Austriacopithecus weinfurthi</i>
Ind I	Neudorf an der Marche,	m-l. Miocene	Zapfe, 1958	<i>Pliopithecus vindobonensis</i>
Ind II	Czech Republic	m-l. Miocene	Zapfe, 1958	<i>Pliopithecus vindobonensis</i>
IGF2011V	Baccinello, Italy	l. Miocene	Hürzeler, 1958	<i>Oreopithecus bambolii</i>

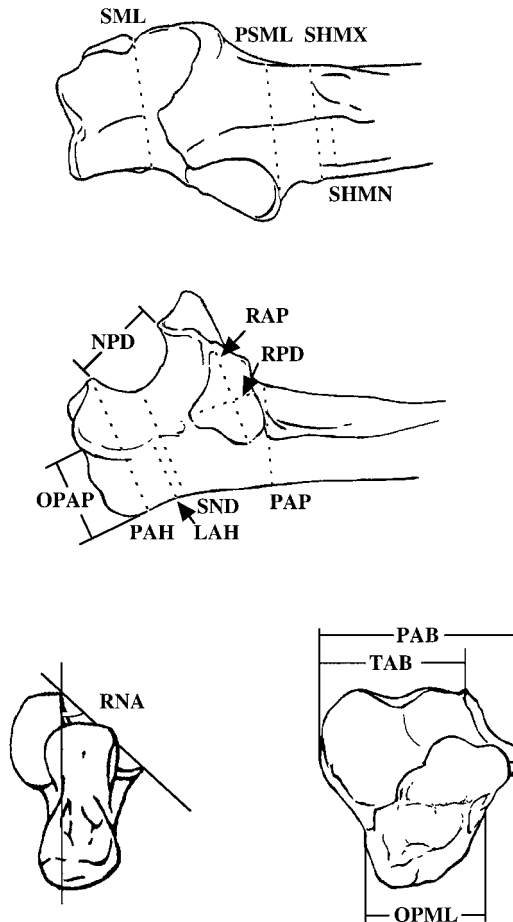


Fig. 3. Line drawing of a gorilla proximal ulna in anterior, lateral, and proximal views, illustrating most of the measurements used in this analysis (MAH, not shown, is measured on the medial side opposite LAH). RNA is shown on a line drawing of the proximal view of a *Papio* ulna. Measurement abbreviations are described in Table 3.

Richmond and Jungers, 1995). Ulnar shape is computed here as the ratio of each variable to the GM (Darroch and Mosimann, 1985; Jungers et al., 1995).

Multivariate summary statistics are used here to assess the morphological affinities of the extant and fossil ulnae. Because of the variability in preservation of the fossil sample, canonical variates analyses, or CVAs, are calculated for two subsets of the raw and size-adjusted data. In the first, the entire suite of measurements (except the angular measure, RNA) and only the most complete

fossils are included. The second CVA is based on a subset of the measurements to allow the inclusion of the full fossil sample (Table 3). The fossil specimens were included in the CVA a priori to allow them to contribute to the canonical shape space (Oxnard, 1972; Corruccini, 1978). SAS and SYSTAT statistical packages were employed to calculate and plot the CVAs. The variables with the greatest discriminatory power among the extant and fossil taxa (i.e., those with the highest between-group canonical structure coefficients; Klecka, 1980) provide a focus for the subsequent investigation into the structural and functional differences

TABLE 3. Measurements included in this analysis (see also Figure 3)

Abbreviation	Description
PAB*†	Proximal articular mediolateral breadth of radial notch and trochlea
TAB*	Trochlear articular mediolateral breadth
PSML*†	Proximal shaft mediolateral width at distal margin of radial notch
PAP*†	Proximal shaft anteroposterior thickness at distal margin of radial notch
RAP*	Radial notch anteroposterior thickness
RPD*	Radial notch proximodistal length
PAAP*†	Proximal articular anteroposterior thickness at coronoid process
SND*†	Sigmoid notch depth; minimum anteroposterior thickness of sigmoid notch
SML*†	Sigmoid notch mediolateral width
PAH	Proximal articular anteroposterior thickness at anconeal process
OPAP	Olecranon process anteroposterior thickness
OPL	Olecranon process length from anconeal process
NPD	Sigmoid notch proximodistal length from proximal to distal beaks
OPML	Olecranon process mediolateral breadth
SHMN	Minimum mediolateral width of shaft anterior to brachialis insertion
SHMX	Maximum mediolateral width of shaft including brachialis insertion
MAH*	Medial anteroposterior articular thickness from posterior border of medial articular surface to posterior border of shaft
LAH*	Lateral anteroposterior articular thickness from posterior border of lateral articular surface to posterior border of shaft
RNA	Radial notch angle (in degrees) relative to anteroposterior plane

\* Subset of measurements used in analyses involving the entire fossil sample.

† Subset of measurements used in calculation of geometric mean for full fossil sample.

Many of these measures are adapted from Begun (1992a). Measurements are shown in mm unless otherwise indicated.



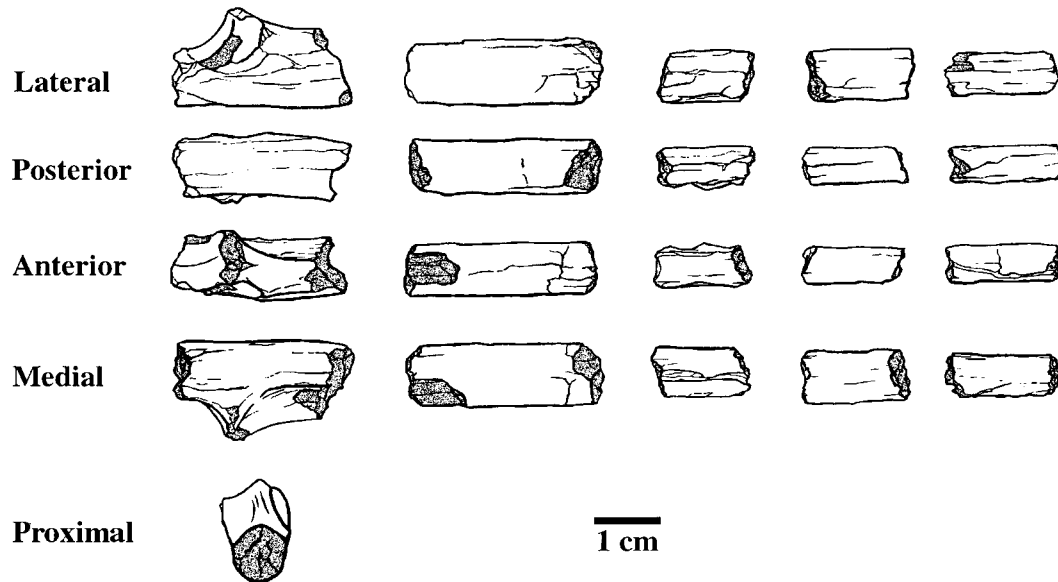


Fig. 4. Line drawing of FJ-18SB-68. Features in common with apes include the laterally facing radial notch, incipient trochlear keel, and deep depression for insertion of the brachialis muscle.

between these groups (McHenry and Corrucini, 1975; Oxnard, 1975).

#### Description

FJ-18SB-68 is comprised of five fragments representing much of a right ulna approximately the size of that of a male howler monkey or spider monkey (roughly 8 kg; Jungers, 1985; Fig. 4). It was recovered at FJ-18 in September, 1992, by J.K. The four shaft fragments are roughly elliptical in cross-section, with slightly flattened medial borders. Two of the distal fragments have suffered from post-depositional erosion of the bone surface. None of the fragments articulate with one another; nevertheless, it appears that much of the ulnar shaft is preserved. It is not possible to determine whether FJ-18SB-68 is an adult or juvenile because both the proximal and distal epiphysal regions are missing.

The proximalmost fragment preserves the distal half of the sigmoid notch, the radial notch, and about a centimeter of the proximal shaft. The trochlear notch does not exhibit the strongly developed midsagittal keel characteristic of extant hominoids, especially great apes and humans (Napier and Davis, 1959; Fleagle, 1983; Rose, 1988).

However, the slightly raised midline of the trochlear notch is unlike that of modern nonhominoid anthropoids such as *Alouatta* and *Presbytis*; rather, it resembles the incipient trochlear keel in early hominoids such as *Proconsul heseloni* and *Turkanapithecus kalakolensis* (Leakey et al., 1988; Rose, 1993, unpublished manuscript; Larson, 1993). The trochlear notch is deep relative to the height of the proximal shaft and slopes gently anteriorly towards the coronoid process, like that of many arboreal quadrupeds and unlike terrestrial monkeys whose notch curves more strongly. The coronoid is narrow relative to extant apes and does not appear to project far anteriorly above the shaft, although the tip of the coronoid process has been eroded. The medial margin of the trochlear notch, also slightly eroded, appears to have possessed a sharp edge. The lateral border, on the other hand, curves posteriorly to join the lateral surface of bone without interruption (Fig. 4). Neither the medial nor lateral borders of the articular surface extend very far posteriorly towards the back of the shaft.

The very flat radial notch is positioned laterally on the ulnar shaft such that little of it can be seen from an anterior view (Fig. 4).

In this regard, FJ-18SB-68 deviates from the morphology seen in most quadrupedal anthropoids, in which the radial notch faces *antero*-laterally and covers about half of the width of the ulnar shaft (Fig. 5c). The latter radio-ulnar configuration is seen in *Aegyptopithecus* and appears to be primitive for catarrhines. The edges of the articular surface do not project laterally from the shaft, thereby providing little or no support posteriorly for the head of the radius.

Immediately distal to the coronoid and radial notch, the shaft possesses a deep groove on the medial side for the insertion of *m. brachialis* (Fig. 4). The supinator crest is distinct, as in *Turkanapithecus* (Rose, 1997), but not as well developed as in living great apes, *Dryopithecus*, and *Austriacopithecus* (Klein Hadersdorf; Table 2). In general, FJ-18SB-68 most closely resembles *T. kalakolensis* and *P. heseloni*, but differs in its slightly more laterally facing and less rugose radial notch and its more extensively excavated brachialis depression.

## RESULTS

We initially investigate complete proximal ulnae of living and some fossil anthropoids. An analysis of complete ulnar morphology reveals how well the measurements used here discriminate among extant taxa in terms of function and phylogeny. It provides the context for the following multivariate analysis based on more fragmentary remains, which permits consideration of a more diverse fossil sample, including the Fejej specimen, but suffers in discriminatory power.

### Complete measurement set

The CVA of shape variables (ratios of variables to GM) separates extant anthropoids into three major clusters: hominoids, cercopithecoids, and platyrrhines (Fig. 6). CAN1 discriminates well between apes and all other nonhominoid anthropoids, while CAN2 separates platyrrhines (*Ateles* and *Aouatta*) from catarrhines. This is not a reflection of size differences. The position of the monkey-sized gibbons in the cluster of the much larger great apes underscores this fact. Correlations between the group centroids for each shape variable and the canonical axes are shown in Table 4.

The third canonical axis (not shown), representing 11.6% of the canonical variation (CAN4, 3.3%), distinguishes gibbons from all other anthropoids, based on their relatively large radial notches (RPD, RAP), shallow depth posterior to the sigmoid notch (SND), and shallow (AP) olecranon process (OPAP).

The shape of the proximal ulna is distinct in each of the three major groups, suggesting fundamental differences in elbow function. The platyrrhine ulnae examined here are characterized by being relatively narrow (mediolaterally, or ML) proximally in both the shaft and articular surface, with antero-posteriorly (AP) short radial notches and long (proximodistally, or PD), narrow olecranon processes (Fig. 6 and Table 4). The cercopithecoid ulna is like that of platyrrhines in many of these features (i.e., cercopithecoids fall on the platyrrhine side of CAN1) but are generally more extreme in each variable. The olecranon process is long and deep, the sigmoid notch is exceptionally narrow and deep, the coronoid process does not project markedly, and the radial notch is AP elongated (see also Bown et al., 1982; Harrison, 1987; Rose, 1988; Ciochon, 1993). These features are uniquely combined in cercopithecoids with the broad, deep shafts and articular surfaces and the relatively short sigmoid notch length (NPD) that characterize modern catarrhines. Hominoids also possess these catarrhine features but are distinguished from all other anthropoids in having a relatively large trochlear surface, broad sigmoid notch that is well buttressed posteriorly, broad, but otherwise small olecranon process, and projecting coronoid process (see also Harrison, 1987; Fleagle and Kay, 1987; Rose, 1988).

The fossil ulnae are encompassed by the total ulnar shape variation displayed by the extant taxa (Fig. 6). *Aegyptopithecus* and *Pliopithecus* most closely resemble the living New World monkeys in this sample and appear to lack the specializations of either the extant cercopithecoids or hominoids (Fleagle et al., 1975; Fleagle, 1983, 1988). The Miocene hominoids *Turkanapithecus* and *Proconsul nyanzae* clearly cluster with the quadrupeds along CAN1 and the catarrhines on CAN2, but do not overlap with the

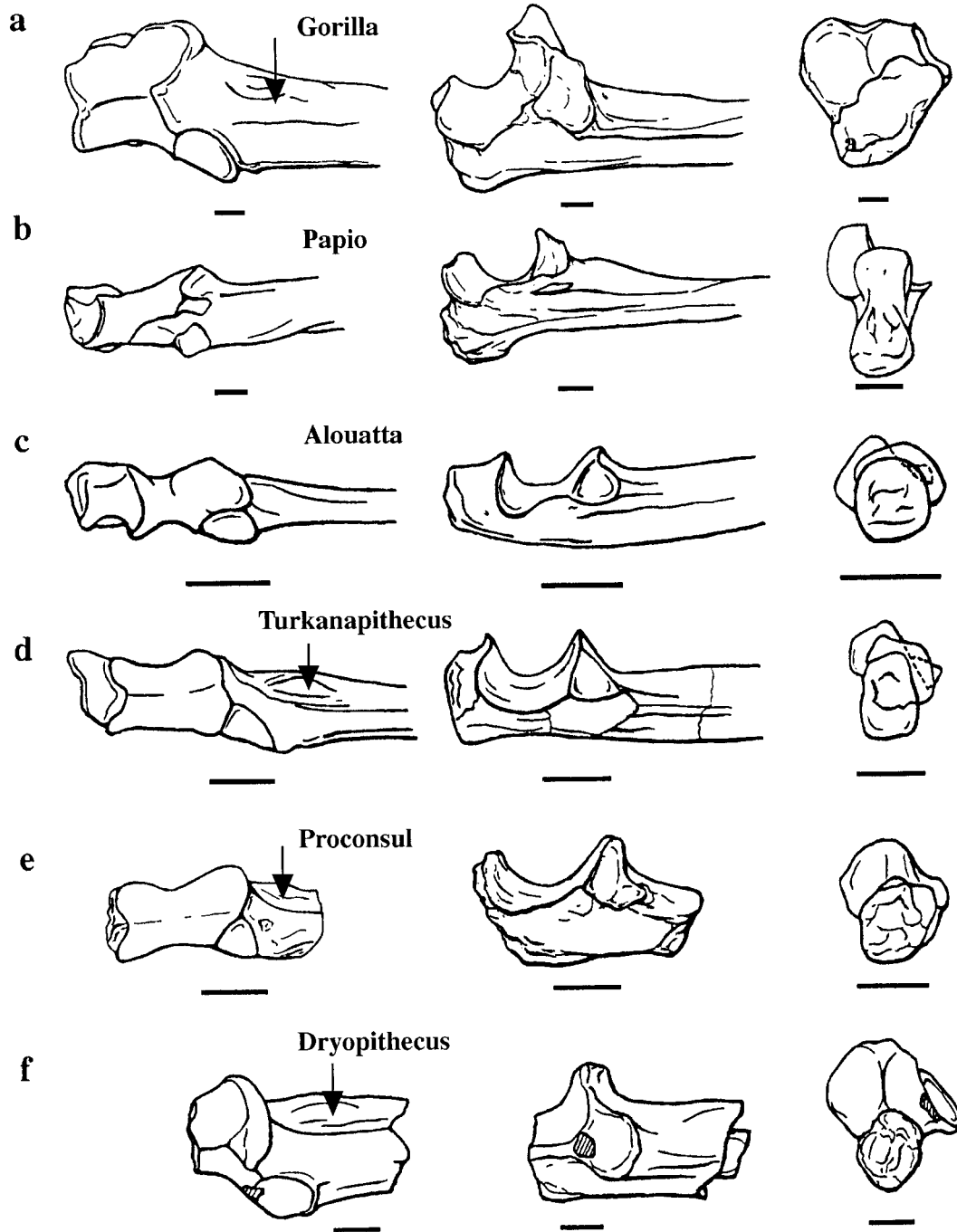


Fig. 5. Line drawings of representative ulnae of extant and fossil primates: a) *Gorilla gorilla*, b) *Papio anubis*, c) *Alouatta sp.*, d) KNM-VVK 16950R, *Turkanapithecus kalakolensis*, e) KNM-RU 2036, *Proconsul heseloni*, and f) RUD22, *Dryopithecus brancoi*. Shown in anterior, lateral, and proximal views, respectively. *Turkanapithecus* is a reversed drawing of the left ulna. Each scale bar represents approximately 1 cm. Arrows denote the deep depression for the brachialis muscle insertion.



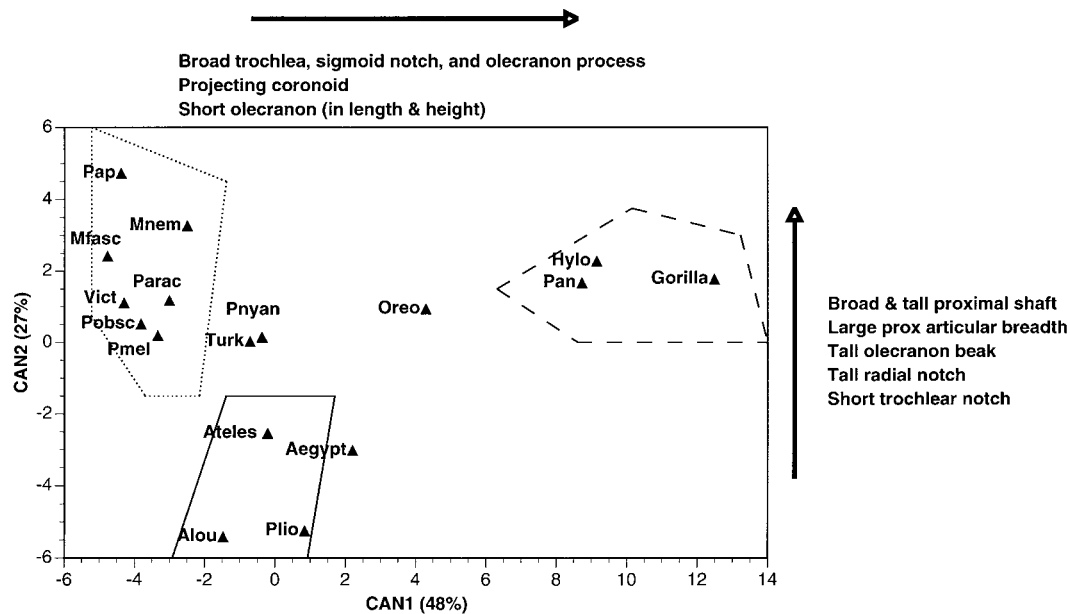


Fig. 6. Canonical variates analysis (CVA) of shape variables of the complete set of proximal ulna measurements. The most influential variables for CAN1 (top) and CAN2 (right) are listed. Also see Table 4. The extant samples and only the more complete fossils are included. Note that the platyrrhines (solid lines), here *Alouatta* and *Ateles*, are separated along CAN2 from the catarrhines above. The apes (dashed lines) cluster at the right end of the plot and cercopithecoids (dotted lines) are in the upper left. Group envelopes (i.e., solid, dashed, and dotted lines) roughly represent the range of individuals in each group. *Aegyptopithecus* and *Pliopithecus* re-

semble New World monkeys and appear to represent the primitive condition; *Turkanapithecus* and *Proconsul* are clearly catarrhine in their ulnar shape, but not derived towards Old World monkeys or apes. *Oreopithecus* is the only ape-like fossil. Abbreviations: Aegypt = *Aegyptopithecus*; Alou = *Alouatta*, Hylo = *Hylobates*, Mfasc = *Macaca fascicularis*, Mnem = *M. nemestrina*, Oreo = *Oreopithecus*, Pan = *Pan troglodytes*, Pap = *Papio*, Parac = *Paracolobus*, Plio = *Pliopithecus*, Pmel = *Presbytis melalophus*, Pnyan = *Proconsul nyanzae*, Pobs = *Presbytis obscura*, Turk = *Turkanapithecus*, Vict = *Victoriapithecus*.

TABLE 4. Correlations between group centroids of shape variables and canonical axes 1–3 for full set of variables

Variable	CAN1	CAN2	CAN3
PABS	0.592	0.686	0.331
TABS	0.976	0.020	-0.025
PSMLS	0.526	0.740	0.093
PAPS	0.181	0.658	-0.378
RAPS	-0.420	0.659	0.576
RPDS	0.157	-0.562	0.640
SNDS	0.711	0.309	-0.588
SMLS	0.921	-0.020	0.319
SHMXS	0.500	0.782	-0.050
MAHS	0.568	0.315	-0.487
LAHS	0.278	0.660	-0.498
PAAPS	0.728	0.551	-0.217
SHMNS	-0.147	0.757	0.241
PAHS	0.271	0.661	-0.487
OPAPS	-0.723	0.021	-0.596
OPLS	-0.706	-0.682	0.056
NPDS	0.116	-0.622	0.277
OPMLS	0.883	-0.161	0.371
Eigenvalue	29.578	16.837	7.132
% variance explained	48.1	27.4	11.6

morphological ranges of either the Old World or New World monkeys. They appear to be less specialized in their ulnar proportions than either the Old World monkeys or apes (Rose, 1983). *Paracolobus chemeroni* and *Victoriapithecus macinnesi*, on the other hand, are morphologically cercopithecoids. Ciochon (1993) has shown that, when considering cercopithecoids alone, colobines and cercopithecines are further distinguishable with ulnar morphology. *Oreopithecus* is the only fossil ulna in this sample that can be described as ape-like. It is somewhat intermediate, but most like the chimpanzee, corroborating previous descriptions of its hominoid-like postcranial morphology (Hürzeler, 1958; Straus, 1961; Szalay and Delson, 1979; Harrison, 1986; Jungers, 1987; Sarmiento, 1987). Thus, multivariate analysis based on the shape of the complete proximal ulna

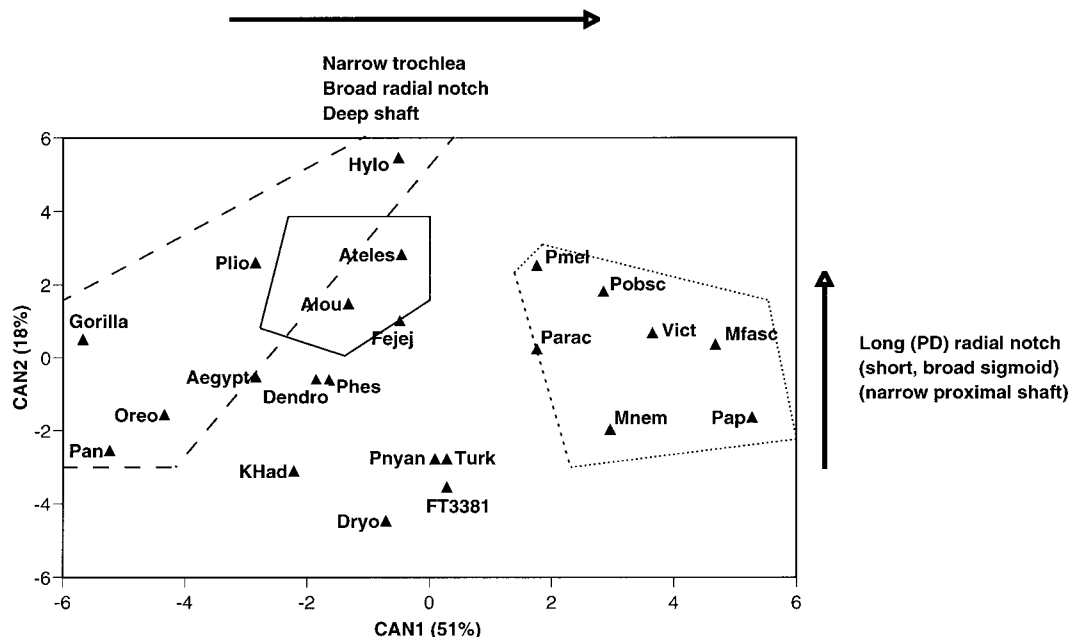


Fig. 7. Canonical variates analysis (CVA) of shape data for the subset of ulnar variables that allows inclusion of the full fossil sample (see Table 2). The most influential variables for CAN1 (top) and CAN2 (right) are listed. Variables in parentheses are less influential; see Table 5 for variable loadings. Outlines around groups roughly represent the observed range of individuals in each group (platyrrhines, solid lines; cercopithecoids, dotted lines; hominoids, dashed lines). Cercopithe-

coids (including *Victoriapithecus* and *Paracolobus*) cluster to the right; gorillas, chimpanzees, and *Oreopithecus* lie on the far left; gibbons, New World monkeys, and a variety of fossils cluster in the center. Abbreviations are listed in Fig. 6, as well as the following: Dendro = *Dendropithecus*, Dryo = *Dryopithecus*, Fejej = FJ-18SB-68, FT3381 = KNM-FT3381; KHad = Klein Hadersdorf (= *Austriacopithecus*?), Phes = *Proconsul heseloni*.

discriminates phylogenetically among anthropoids.

#### Measurement subset with fragmentary fossils

The same analysis was performed on the restricted region of the proximal ulna (the distal half) that is preserved in a much larger fossil sample, including the Fejej fossil. CVAs were first computed for the raw data of the subset of measurements. This analysis essentially discriminated by size on the first axis and separated cercopithecoids on the second axis.

The second CVA, based on shape variables (ratios of variables to the GM; Table 3), discriminates groups according to phylogeny (Fig. 7), although not as clearly as the analysis based on more complete ulnae (Fig. 6). CAN1 successfully discriminates cercopithecoids from other extant and fossil anthropoids (Fig. 7). Cercopithecoids are distin-

guished by their narrow trochleae, anteroposteriorly long radial notches, and deep shafts (Table 5). The great apes represent the opposite extreme, and the New World monkeys and gibbons are intermedi-

TABLE 5. Correlations between group centroids of shape variables and canonical axes 1–3 for subset of variables that permits the inclusion of more fragmentary fossil ulnae

Variable	CAN1	CAN2	CAN3
PABS	0.372	0.115	0.772
TABS	–0.924	0.108	0.210
PSMLS	0.363	–0.297	0.703
PAPS	0.583	0.053	–0.762
RAPS	0.917	0.325	0.104
RPDS	0.024	0.834	–0.240
SNDS	–0.315	–0.569	–0.689
SMLS	–0.702	0.575	0.322
SHMXS	0.242	–0.545	0.682
MAHS	–0.079	–0.321	–0.690
LAHS	0.381	–0.438	–0.346
Eigenvalue	16.446	5.690	4.121
% variance explained	51.1	17.7	12.8

ate (Fig. 7). Although fossils appear to form their own group in the lower center of the plot, the CVA is overwhelmingly influenced by the variation in the extant data. A CVA performed exclusively on the extant sample (not shown) is virtually identical to the one shown in Figure 7 that includes the fossils, indicating that the variation in shape in the extant taxa largely encompasses that in the fossil ulnae (cf. Oxnard, 1972).

It appears that the portion of the ulna preserved by the Fejej specimen is not enough to discriminate clearly among the fossil taxa. However, the CVA allows us to conclude that FJ-18SB-68 lacks the derived proportions of living cercopithecoids and African apes. It clusters near primitive fossil apes (e.g., *P. heseloni* and *Dendropithecus*) and platyrrhines (here, *Alouatta* and *Ateles*), suggesting arboreal quadrupedalism with some forelimb mobility. The functional and phyletic affinities will be discussed in more detail below with respect to specific morphological traits.

### DISCUSSION

The results presented here reinforce those of previous studies that the elbow joint is one of the most distinctive regions of the postcranium in anthropoids (McHenry and Corruccini, 1975; Fleagle, 1983; Rose, 1988). The shape of the proximal ulna alone distinguishes platyrrhines from catarrhines and, within the latter group, cercopithecoids from hominoids. The distinctive ulnar morphology of each group is presumably related to fundamental differences in elbow function in each of these groups. The functional significance of certain ulnar characteristics are discussed below. The phyletic affinities of FJ-18SB-68 and other fossil ulnae are then examined in light of derived features that characterize extant groups.

#### Catarrhines

Few characteristics of the elbow have been identified as derived for catarrhines. They include the loss of the entepicondylar foramen (Fleagle, 1983; Harrison, 1987) and a non-translatory humeroulnar joint (Rose, 1988). This analysis contributes at least two additional features in which modern catarrhines are derived relative to platyrrhines

and primitive fossil catarrhines (*Aegyptopithecus* and *Pliopithecus*; see Fig. 6): catarrhine ulnae 1) are more robust, with broad and deep shafts and articular surfaces, and 2) have relatively short (PD) sigmoid notches (Fig. 5). The functional significances of these features are not clear.

Another non-metric feature of the ulna of functional and phylogenetic import is the morphology of the proximal radioulnar joint. The position of the radius relative to the ulna varies widely in anthropoid primates (Sarmiento, 1985; Rose, 1988). New World monkeys like *Alouatta*, and fossils like *Aegyptopithecus* (Fleagle et al., 1975), represent the primitive form in which the radial head lies anteriolaterally to the proximal ulna and anteriorly overlaps with roughly one half of the width of the ulnar shaft (Fig. 5c, anterior view). Therefore, the radius is partially buttressed by the ulnar shaft medially and posteriorly. The oval, tilted radial head in these taxa fits in the radial notch most tightly when the forearm is fully pronated; this "close-packed" fit is the position of maximum stability (Rose, 1983, 1988). Cercopithecoids and hominoids (especially great apes) are both derived in their radial notch morphology (Rose, 1988, 1993).

#### Cercopithecoids

The elbow joint of cercopithecoids displays a suite of derived features (Rose, 1983, 1988; Harrison, 1987; Ciochon, 1993). Those specific to the ulna include: an unevenly curved radial notch; limited, laterally facing area of the trochlear notch for articulation with lateral side of humeral trochlea; anteriorly facing radial notch (Rose, 1988); wide radial notch articular surface; radial notch positioned more posteriorly; and a narrow trochlear articular surface (Ciochon, 1993). The multivariate analysis here is consistent with these studies. The cercopithecoid ulna is derived in its exceptionally narrow distal trochlea and sigmoid notch (see Fig. 5a-c). Multivariate results also point to the narrow, deep olecranon process, and a deep (as well as narrow) sigmoid notch. Note that discussing character "states" resulting from the multivariate analyses often requires imposing categorical boundaries to continuous traits (Ciochon, 1993). While few of these

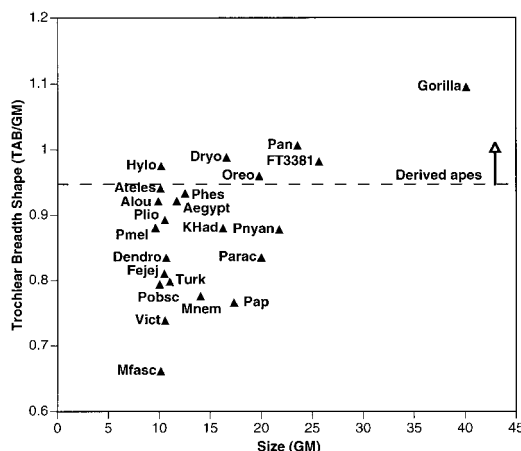


Fig. 8. Trochlear breadth shape reflects the width of the coronoid process relative to the size (GM) of the ulna. Living apes and more derived fossil apes have much broader coronoid processes, and trochleae in general, than other anthropoids.

traits are discrete, they are nonetheless important in characterizing ulnar shape.

The functional significance of olecranon process morphology has been discussed in some detail (Oxnard, 1963; Bown et al., 1982; Fleagle, 1988; Harrison, 1989; Hildebrand, 1995). In anthropoids, an elongated olecranon is indicative of quadrupedalism, with arboreal quadrupeds possessing the longest olecranon and terrestrial quadrupeds possessing a posteriorly expanded (and, therefore, deep) olecranon process, in both providing effective leverage for the *m. triceps brachii*.

Rose (1983, 1988) noted that the narrow trochlear articular surface of cercopithecoids is partially convergent on that of more cursorially adapted mammals (Jenkins, 1973; Hildebrand, 1995; see also Conroy, 1976). Reduction in trochlear size may be related to increased radial head size, in which force transmission is shifted from the ulno-humeral to the radio-humeral joint (Conroy, 1976; Hildebrand, 1995). Trochlear breadth shape is plotted in Figure 8, and cercopithecoids exhibit the narrowest trochleae in most cases. Generally, the more terrestrial taxa have narrower ulnae, but *M. fascicularis* appears to have the narrowest trochlea in this sample (Fig. 8). This is partly due to the flaring coronoids in *M.*

*nemestrina* and *Papio* that influenced measures of trochlear width taken here. These taxa have very narrow trochleae near the base of the trochlear notch and the expanded coronoid may be allometrically related to weight support in these larger-bodied monkeys.

Recent experimental data shed new light on the functional significance of the cercopithecoid trochlear articular surface. In Old World monkeys, the trochlear articular surface faces medially at the coronoid beak, spirals anteriorly to the base of the notch, and wraps laterally onto the olecranon process (see *Papio* in Fig. 5). Rose (1983) notes that the humeral articulation of cercopithecoids is designed to withstand primarily medial forces tending to adduct the ulna (see also Jenkins, 1973). All cercopithecoid taxa examined here exhibit this morphology, but the semi-terrestrial baboon ulna appears most specialized in the extent of articular surface dedicated to resisting this medially directed force on the forearm. Experimental data corroborate this interpretation. Schmitt (1994) documented medial ground reaction forces in the baboon while walking on the ground and Demes et al. (in press) recorded mediolateral bending as the dominant stress regime in vivo in the macaque ulna during normal terrestrial walking. Therefore, the narrow ulna of cercopithecoids is apparently designed as a stable hinge joint for anteroposterior movements that are accompanied by a regular medially directed force during the stance phase of locomotion. Because of this medial "adducting" ground reaction force, the coronoid portion of the ulnar trochlea is buttressed against the medial lip of the humeral trochlea and the laterally facing olecranon part of the ulnar articulation contacts the heavily developed lateral surface of the humeral olecranon fossa. In effect, the trochlear notch pivots around the proximo-distal axis of the distal humerus during movement about the mediolateral axis. The buttressing that resists this regular medial force may contribute to humeroulnar stability during running. An exaggerated form of this construction can be seen in many cursorial mammals (Hildebrand, 1995).

A number of the characteristic features of the cercopithecoid ulna involve the radial

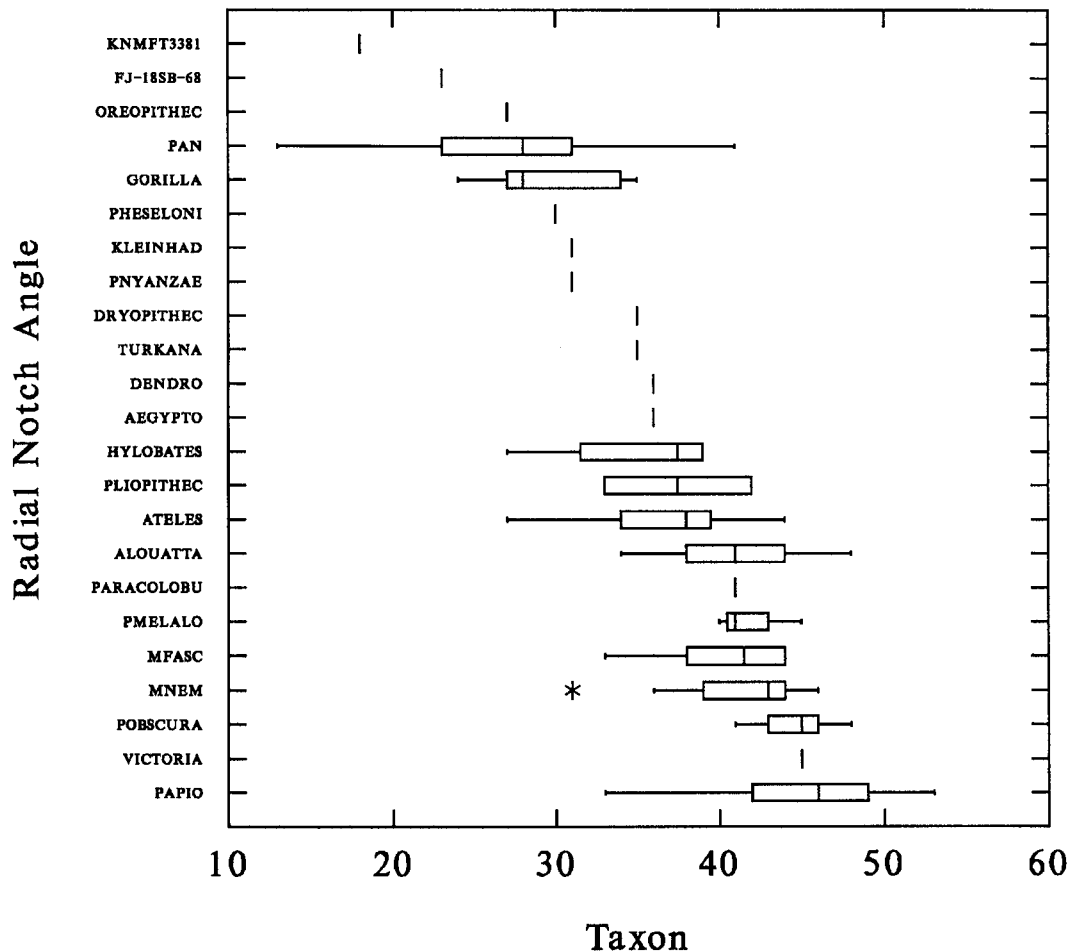


Fig. 9. Box-and-whiskers plots of the radial notch angle for extant and fossil anthropoids. The angle (in a transverse plane) of the radial notch is measured relative to vertical. Among extant taxa, the radial notch of living apes faces most laterally (low angle) and cercopithecoid (especially *Papio*) radial notches face most anteriorly. Note that the hominoid fossils also have low radial notch angles. Each box represents the interquartile range; the inner vertical lines mark the medians. The whiskers show the most extreme values within  $\pm 1.5$  interquartile ranges of the outer edges of the box. Asterisks represent outliers.

notch. The radial notch of semi-terrestrially quadrupedal catarrhines is more deeply excavated (Harrison, 1989; Ciochon, 1993), and Rose (1983, 1988) notes that the anteriorly facing radial notch brings the radius into a position almost directly anterior to the ulna (Fig. 5b). This is almost certainly related to cursorial specializations in the more terrestrial cercopithecoids. When placed in anatomical position on the ulna, the radial head is in near sagittal alignment with the ulna and is solidly buttressed posteriorly by the ulna. This configuration, in a much more

specialized form (with the radius directly anterior to the ulna, and often fused), typifies many cursorially adapted mammals, such as artiodactyls, perissodactyls, lagomorphs, and hyracoids (Jenkins, 1973; Hildebrand, 1995). This suggests that anteroposterior forces are critical to elbow morphology in fast-running locomotion.

In an effort to find an objective measure of the observed variation in radius position, radial notch angle was measured here in the extant anthropoid comparative sample (Fig. 9). The angle is not an ideal measure of



radial position (i.e., lateral, anterolateral, and anterior) because of the influence of other structures, such as the height of the coronoid process in some taxa (e.g., *Papio*, see Fig. 5b). There is a great deal of variation in the angle of the radial notch, but cercopithecoids do possess significantly higher angles (t-test,  $P < 0.001$ ) than other groups (Fig. 9). Platyrrhines examined here have intermediate radial notch angles. Among cercopithecoids, the terrestrial quadrupeds possess the largest radial angles (Fig. 9). The radial notches of the most terrestrial cercopithecoids possess two distinct (e.g., *Papio*) or partially connected (*M. nemestrina*) articular facets—one facing almost directly laterally on the lateral surface of the coronoid beak and another facing virtually anteriorly (nearly 90° to the sagittal plane) on the anterior surface of the ulnar shaft. Morphology suggests that taxa with high (more anterior) radial angles are characterized by habitually pronated forearm use (Rose, 1983, 1988; Hildebrand, 1995). This is consistent with the higher radial angles (Fig. 9) and more flattened radial heads (Rose, 1988) found in terrestrial quadrupeds.

In sum, the morphology specific to cercopithecoids appears to reflect adaptations towards terrestriality not seen in other ulnae examined here (see also Harrison, 1989; Ciochon, 1993).

### Hominoids

Ulnar morphology in hominoids has received a considerable amount of attention, resulting in a long list of features identified as derived for hominoids. These include a laterally facing radial notch, relatively short olecranon beak, distally wide trochlear notch, marked median ridge in trochlear notch, surface for articulation with the medial humeral trochlear keel that occupies the whole length of the trochlear notch, extensive area for articulation with humeral lateral keel and surface in the olecranon fossa, reduced olecranon process, strongly developed supinator ridge, relatively low and broad trochlear notch, and a more robust, less bilaterally compressed shaft (Morbeck, 1975; Fleagle et al., 1975; Fleagle and Kay, 1987; Sarmiento, 1985; Harrison, 1987; Rose, 1988, 1997). Despite the numerous studies on the hominoid elbow, the proximal ulna of homi-

noids has not been investigated previously using multivariate methods (of which we are aware). The CVA here identifies features which hominoids share with cercopithecoids as modern catarrhine traits, including the broad and deep shaft and articular surfaces and a relatively short sigmoid notch. Hominoids are distinguished here by their exceptionally wide trochlea and sigmoid notch, depth of bone posterior to the sigmoid notch, and broad but otherwise small olecranon process (see Fig. 6).

Relative trochlear breadth (ratio of trochlear breadth to GM) distinguishes all extant and some fossil apes from other anthropoid taxa (Fig. 8). The broad trochlea is undoubtedly related to the presence of a trochlear keel. The trochlear keel has been argued to be an adaptation for increasing mediolateral and/or rotational stability of humeroulnar joint for climbing/suspensory locomotion in apes (Jenkins, 1973; Sarmiento, 1985; Rose, 1988). This is consistent with the enlarged musculature for pronation and supination, including the ulnar head of *m. pronator teres* typically found in living apes but not in prosimians and monkeys (Howell and Straus, 1933).

Despite substantial variation, extant hominoids have significantly lower radial notch angles (i.e., laterally facing radial notches) than other anthropoids (Fig. 9). These results are broadly similar to measurements taken on hominoid ulnae by Sarmiento (1985); however, our measurements are consistently higher, indicating that slightly different methods may have been used and preclude direct comparisons. Just as the anteriorly facing radial notch is argued to be an adaptation for stability and pronated forearm posture in cercopithecoids, the laterally positioned radius in hominoids is probably associated with forearm rotational mobility (Fig. 5; Jenkins, 1973; Rose, 1983; Sarmiento, 1985). This interpretation is supported by the fact that *Ateles*, a platyrrhine with unusual forearm mobility (Larson, in press), has a laterally facing radial notch comparable to gibbons. A number of possible advantages of forearm rotational mobility have been put forth, including increased proficiency in climbing (Prost, 1965; Stern, 1971; Stern and Oxnard, 1973; Fleagle, 1976; Fleagle et al., 1981; Sar-

miento, 1987), brachiation (Jenkins, 1981), and below-branch suspension (Grand, 1972). Range of rotational motion in cadaveric primates is empirically higher in taxa with more laterally facing radial notches (O'Connor and Rarey, 1979; Sarmiento, 1985). The lateral radial position also suggests that anteroposterior forces either play a lesser role in the hominoid radius or that force is somehow transferred to the highly stabilized humero-ulnar joint. Thus, it appears that the hominoid ulna dedicates a relatively greater proportion of its articular surface to the humerus than to the radius compared to other anthropoids, presumably related to increased mobility (and less weight-transmission?) of the radius.

The abbreviated length of the olecranon process in hominoids has been noted by many (e.g., Oxnard, 1963; Morbeck, 1975; Fleagle et al., 1975; Fleagle, 1983, 1988; Sarmiento, 1985; Harrison, 1987; Rose, 1988). Reduced length (and depth?) of the olecranon process may be necessary to allow the full elbow extension important to suspensory behaviors (Sarmiento, 1987). Although short, the olecranon is broad in apes, probably to maintain adequate surface area for the insertion of *mm. triceps brachii*.

### Evolution of the elbow

The multivariate analysis (Fig. 6) presented here supports previous observations that the ancestral catarrhine ulna more closely resembles platyrrhines than either group of extant catarrhines (Fleagle et al., 1975; Fleagle, 1983; Rose, 1983). This is true of *Aegyptopithecus*, *Pliopithecus*, and *Dendropithecus*, which are all undisputable catarrhines based on derived craniodental morphology (Fleagle et al., 1975; Harrison, 1987; Fleagle, 1988; Simons, 1995). From the fairly generalized morphology observed in *Aegyptopithecus* (Fig. 10), two basic trends follow: one with specializations for terrestriality, including an anteriorly facing and centrally positioned radial notch and a narrow trochlea seen in cercopithecoids, and another with various degrees of specializations for increased forearm rotational mobility, including a laterally facing and positioned radial notch and a wide trochlear notch.

In *Victoriapithecus* and *Paracolobus*, the derived morphology of extant cercopithe-

coids is already present (von Koenigswald, 1969; Szalay and Delson, 1979; Harrison, 1987; McCrossin and Benefit, 1992, 1994). Both fossils possess narrow trochleae (Fig. 8), anteriorly facing radial notches (Fig. 9), and long, narrow olecranon processes. *Victoriapithecus* more closely resembles the cercopithecines, with its more deeply excavated radial notch that is partially separated into two subfacets (Fig. 10). Furthermore, the trochlear surface indicates considerable resistance to the medial adducting force observed in terrestrial but not arboreal locomotion (Schmitt, 1994). This and other features, such as the posteriorly expanded olecranon process, are consistent with interpretations of a semi-terrestrial positional behavior with restricted forearm rotational mobility for *Victoriapithecus* (Fleagle, 1988; Harrison, 1989). The cercopithecine-like morphology in this early cercopithecoid leads us to agree with Ciochon (1993, p. 212) that the "locomotor adaptations of the earliest cercopithecoids must have tended towards cursoriality," and that some of the arboreal adaptations of living colobines may represent secondary adaptations to an arboreal lifestyle (see also Ripley, 1979; Andrews, 1982; Strasser, 1988).

It is clear from the multivariate results (Fig. 7) that the Fejej ulna is not a cercopithecoid, as it lacks a narrow trochlea, broad radial notch, and deep (AP) shaft. With the limited morphology preserved, the multivariate analysis failed to discriminate the other extant and fossil anthropoids reliably. Phenetically, the Fejej ulna is most similar to *Pliopithecus*, *Turkanapithecus*, *Aegyptopithecus*, and *Dendropithecus*—a UPGMA clustering analysis (not shown) links FJ-18SB-68 with these taxa to the exclusion of all others, including extant taxa. However, it differs from *Pliopithecus* and *Dendropithecus*, which do not possess the prominent depression (or "medial buttressing," Rose, 1997) for the insertion of brachialis exhibited by FJ-18SB-68 (Fig. 4). Furthermore, *Pliopithecus* is not known from Africa, unless the distal humerus from Moghara (Simons, 1994) is considered to be *Pliopithecus*. The large brachialis depression is present in *Aegyptopithecus* and primitively retained in fossil and extant apes, including proconsulids (see *P. nyanzae* and *P. heseloni*) and *Turkanapithe-*

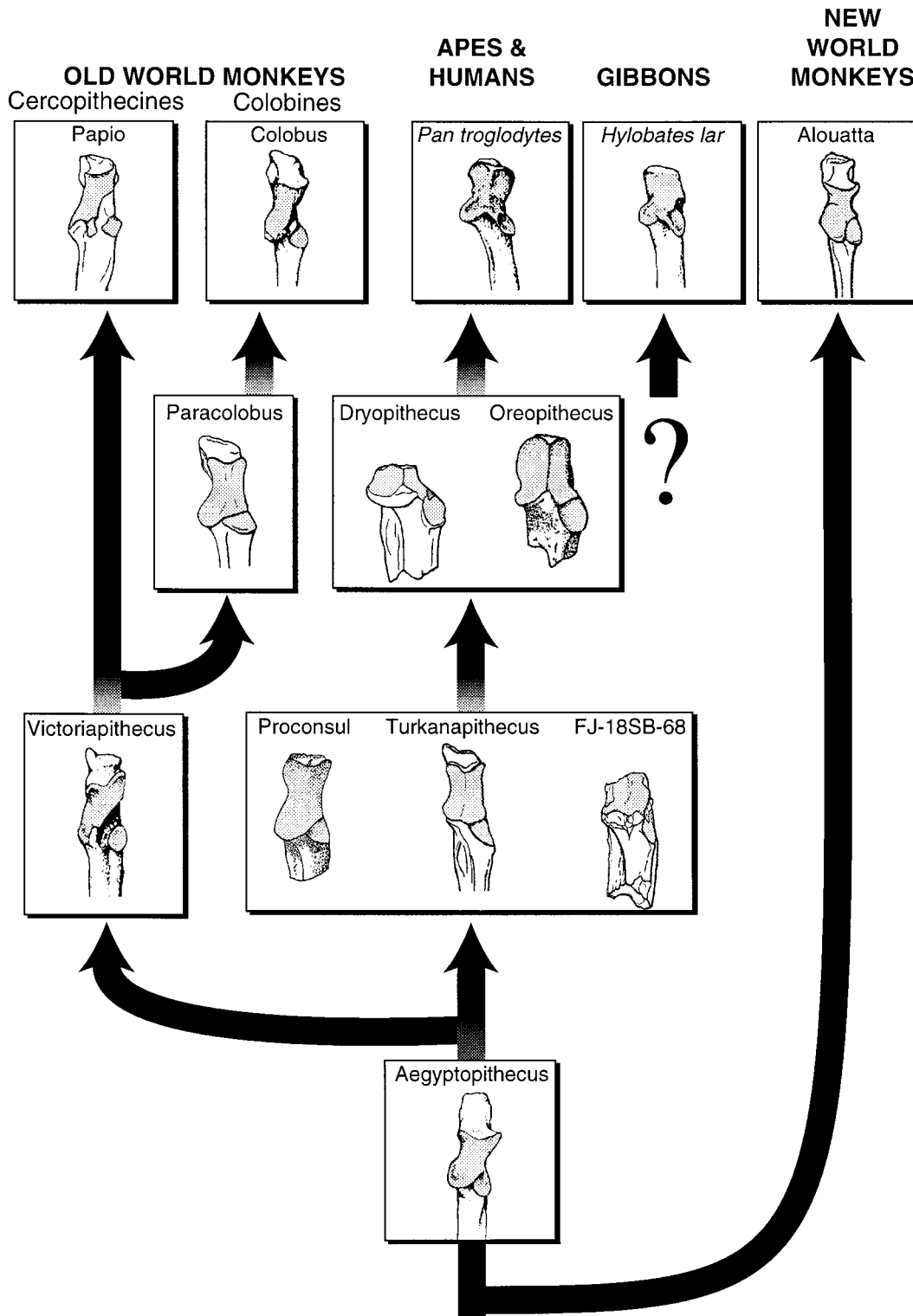


Fig. 10. A phylogeny of Oligocene and Miocene catarrhines based on morphology of the ulna.

cus (Figs. 5 and 9; Rose, 1983, 1997), and suggests the presence of a large brachialis muscle for powerful forearm flexion in these taxa. The trochlea of the Fejej ulna is not wide, as in extant apes, but resembles other Miocene forms such as *Turkanapithecus* and *Dendropithecus* (Fig. 8). The radial notch of FJ-18SB-68 is extreme in its lateral orientation and is one of the only features linking it with extant hominoids (Fig. 9). Like *Turkanapithecus* and *Proconsul*, the midline of the trochlear notch in the Fejej ulna is slightly raised and may be considered an incipient trochlear keel. Of known fossil ulnae, that of *Turkanapithecus* is most similar to FJ-18SB-68, and not unreasonable biogeographically.

Locality FJ-18 may be contemporaneous with the nearby site of Buluk in northern Kenya (Leakey and Walker, 1985; Tiffney et al., 1994). The primates at Buluk include *Prohylobates* sp., *Simiolus enjiessi*, *Afropithecus turkanensis* (Leakey et al., 1988), and possibly *Limnopithecus evansi* (Rose et al., 1992). Both sites are geographically and temporally close to Kalodirr, a 16–18 My-old locality west of Lake Turkana, Kenya, that has yielded *Turkanapithecus* remains as well as *Afropithecus* and *Simiolus* (Leakey and Leakey, 1986). The morphological similarities and approximate contemporaneity of Fejej with Kalodirr suggest that FJ-18SB-68 may represent *Turkanapithecus*, but the fragmentary nature of the fossil ulna does not allow us to rule out other possibilities.

The morphology of the Fejej ulna appears much like other primitive Miocene hominoids (i.e., *Proconsul*, *Turkanapithecus*, "*Austriacopithecus*") and functional interpretations are similar. In overall shape, the Fejej ulna resembles arboreal quadrupeds (Fig. 7), without the narrow trochlea and anteriorly facing radial notch of terrestrial quadrupeds nor the wide trochlea and well-developed median keel of living apes. Rose (1983) points out that the functional morphology of the primitive Miocene apes cannot be considered ape-like or monkey-like (see also Rose, 1993, 1994; Ward et al., 1991, 1993). Rose (1988, 1993) and Ward et al. (1993) agree that *Turkanapithecus* and *Proconsul* are arboreal quadrupeds, but do not consider extant monkeys as appropriate behavioral analogs (contra Andrews and Pilbeam, 1996).

They reconstruct slow, deliberate climbing as important components of their locomotor repertoire, and this seems to be the case in the Fejej ulna and "*Austriacopithecus*" (Begun, 1992a) as well. This is consistent with the lateral orientation and position of their radial notches (Figs. 4, 5, 10), moderately broad trochleae (Fig. 8), poorly developed trochlear keel (Figs. 4, 5), and large brachialis insertions for strong elbow flexion.

The development of an ulnar trochlear keel and spool-shaped humeral trochlea may be related to biomechanical consequences of tail loss in these large arboreal quadrupeds (Richmond, unpublished ms.; Kelley, 1995). Forearm pronation and supination may play an important role in maintaining balance above a branch, especially without the help of a tail (Larson and Stern, in prep). If this is the case, then features related to forearm rotational mobility (e.g., laterally facing radial notch, enlarged rotational musculature, including an ulnar head of *m. pronator teres*) and humero-ulnar stability (widened spool-shaped trochlea and a trochlear keel) that are typically associated with climbing and suspension may have evolved in arboreal quadrupedal ape ancestors as an adaptation for above-branch balance.

The trend towards powerful forearm flexion, broad trochleae, and displacement of the radius from an anterior position to a more lateral one is most strongly expressed in extant great apes. Of the fossil ulnae considered here, only *Dryopithecus*, *Oreopithecus*, and KNM-FT 3381 have trochlea as wide as living apes (Fig. 8). The wide trochlea is undoubtedly related to the presence of a trochlear keel and *Dryopithecus* and *Oreopithecus* are the only fossil apes examined here that possess a well-developed trochlear keel. KNM-FT 3381 is unusual in that it does not possess a trochlear keel, but has an exceptionally broad coronoid. This enigmatic specimen has been considered as "possibly hominoid" (Rose, 1983, p. 190), possibly oreopithecoid (Harrison, 1992), and attributed to *Kenyapithecus wickeri* (Kelley and Pilbeam, 1986) and *Hyainailouros sulzeri* or *Megistotherium* (Pickford, cited in Senut, 1989); it does appear to be a primate (Kitko and Richmond, 1997). If it does repre-



sent *Kenyapithecus*, then it exhibits a strange mixture of features (and is too large to match with the distal humerus, KNM-FT 2751). The laterally facing radial notch (Fig. 9), wide trochlea (Fig. 8), and deep buttressing posterior to the sigmoid notch are consistent with the ape-like descriptions of other *Kenyapithecus* forelimb remains from Maboko Island (McCrossin and Benefit, 1997a). On the other hand, the narrow base of the sigmoid notch, lack of a median trochlear keel, narrow and deep shaft, and expanded coronoid resemble the condition in quadrupeds (terrestrial in some features), morphology that is consistent with a suite of clear terrestrial features (e.g., retroflected humeral curvature, posteriorly directed medial epicondyle, long and retroflected olecranon process, dorsal transverse ridge on metacarpal, and relatively straight phalanges; Richmond, 1995; McCrossin and Benefit, 1997b). Additional work on this fossil ape will hopefully clarify the functional and phyletic position of *Kenyapithecus*.

The phyletic position of *Oreopithecus* has long been debated because of the combination of primitive craniodental features and unusual dentition (Simons, 1960; Delson and Andrews, 1975; Szalay and Delson, 1979; Harrison, 1986) and the apparently derived postcranial similarities with living hominoids (Hürzeler, 1958; Szalay and Delson, 1979; Harrison, 1986; Jungers, 1987; Sarmiento, 1987; Harrison and Rook, 1997). In this multivariate analysis, *Oreopithecus* does not fall within the range of extant hominoids examined here (Fig. 6); however, it is the most ape-like in this sample, particularly when derived hominoid features are considered (Fig. 10). These are a well-developed trochlear keel, wide trochlea, laterally facing radial notch, and short, broad olecranon, among others (Rose, 1997; Harrison and Rook, 1997).

Whatever the phylogenetic affinities, *Oreopithecus* was undoubtedly very ape-like in terms of locomotor behavior, with a great deal of below-branch suspension and clambering (see also Jungers, 1987; Fleagle, 1988).

Unlike *Oreopithecus*, *Dryopithecus* is generally allied with great apes based on cranial and postcranial morphology (Andrews

and Martin, 1987; Begun, 1992a,b, 1993; Moyà-Solà and Köhler, 1996; Begun and Kordos, 1997; but see McCrossin and Benefit, 1994). In the limited ulnar proportions available, it does not clearly ally with the great apes (Fig. 7), but other characteristics lead us to agree with its hominoid status. Namely, it shares with extant apes the well-developed trochlear keel, laterally positioned and oriented radial notch, broad trochlea (Fig. 8), and numerous features from other parts of the skeleton (Moyà-Solà and Köhler, 1996). *Dryopithecus*, too, most likely spent a considerable amount of time in climbing and suspensory behaviors (see also Begun, 1988, 1993; Moyà-Solà and Köhler, 1996).

## SUMMARY

New fossil ulnar remains represent the first Miocene ape from Ethiopia. Multivariate analyses presented here support previous observations that the ancestral condition for the elbow region of catarrhines is basically platyrrhine-like, rather than like that of either extant catarrhine group. From this fairly generalized template, two basic trends have developed: one toward restricted forearm rotational mobility and more habitually pronated forearms, as seen in living and fossil cercopithecoids, and another toward greater forearm rotational mobility leading to modern hominoids. Fossil taxa like *Victoriapithecus* and *Paracolobus* already possess the derived ulnar morphology that characterizes extant cercopithecoids. This morphology includes a very narrow and short trochlear notch, more anteriorly facing (and more centrally positioned) radial notch, long and deep olecranon process, and relatively robust proximal shaft.

Fossil ulnae of the Miocene, including those of *Turkanapithecus*, *Proconsul*, and FJ-18SB-68 share with extant hominoids a laterally positioned and oriented radial notch and slightly more of a trochlear keel than seen in most extant monkeys. These characteristics, along with the retention of a large, medial depression for the insertion of *m. brachialis*, suggest increased rotational mobility and use of the forearm in nonpronated hand postures. This functional anatomy is



consistent with an increased role of climbing in an otherwise arboreal quadrupedal life-style and represents what may be a grade of locomotor adaptation in these early-middle Miocene primitive apes.

*Oreopithecus* and *Dryopithecus* share additional features with living hominoids, including a true trochlear keel and the accompanying increase in trochlear breadth, projecting coronoid beak, and markedly reduced olecranon process. These features are presumably related to elbow joint stability in a wide range of supinated-pronated hand postures and full elbow extension and stability in suspensory postures, especially in association with relatively large body size. This analysis supports the suggestion that many of the suspensory and, especially, climbing features of extant hominoids are further developments of earlier catarrhine forelimb adaptations.

#### ACKNOWLEDGMENTS

Casts of KNM-WK16950R and KNM-WK17171I-M were kindly loaned by Dr. M.D. Rose, and a cast of RUD22 was loaned by Dr. D.R. Begun. We thank Dr. R.W. Thorington, Jr., Curator of Mammals at the Smithsonian Institution's National Museum of Natural History, Dr. Ross MacPhee, Curator of Mammals at the American Museum of Natural History, and Dr. Meave Leakey, Director of Palaeontology at the National Museum of Kenya, for permission to examine the specimens in their care. We are especially grateful to T. Terfa and B. Asfaw for permitting this fieldwork in 1990, and Drs. K. Begashaw and C. Tesfatsion for permission in 1992. T. White (University of California, Berkeley) and G. Suwa (University of Tokyo) suggested that J.G.F. work in the Fejej area and provided invaluable advice and assistance. T. Bown (U.S. Geological Survey), T. Rassmusen (Washington University, St. Louis), Z. Assefa (SUNY, Stony Brook), S. Yirga (Addis Ababa University), T. Hagos, A. Nagesha, C. Tilahun, and M. Fisseha (Ministry of Culture and Sports Affairs, Ethiopia) contributed greatly in the success of the fieldwork. The artwork in Figures 3, 4, and 5 was prepared by William and Barry E. Yee and B.G.R.; Luci Betti-Nash prepared Figure 10. We also thank Bill

Jungers, John Polk, and Mike Lague for helpful discussions and statistical advice. Earlier drafts of this paper were improved by comments from Laura MacLatchy, John Polk, Terry Harrison, and two anonymous reviewers.

#### LITERATURE CITED

- Andrews PJ (1982) Ecological polarity in primate evolution. *Zool. J. Linn. Soc.* 74:233–244.
- Andrews PJ, and Martin LB (1987) Cladistic relationships of extant and fossil hominoids. *J. Hum. Evol.* 16:101–118.
- Andrews PJ, and Pilbeam DR (1996) The nature of the evidence. *Nature* 379:123–124.
- Andrews PJ, and Walker AC (1976) The primate and other fauna from Fort Teman, Kenya. In GL Isaac and ER McCown (eds.): *Human Origins: Louis Leakey and the East African Evidence*. Menlo Park, NJ: W.A. Benjamin, pp. 279–304.
- Asfaw B, Beyene Y, Semaw S, Suwa G, White T, and WoldeGabriel G (1991) Fejej: A new paleoanthropological research area in Ethiopia. *J. Hum. Evol.* 21:137–143.
- Begun DR (1988) Catarrhine phalanges from the Late Miocene (Vallesian) of Rudabanya, Hungary. *J. Hum. Evol.* 17:413–438.
- Begun DR (1992a) Phyletic diversity and locomotion in primitive European hominids. *Am. J. Phys. Anthropol.* 87:311–340.
- Begun DR (1992b) Miocene fossil hominids and the chimp-human clade. *Science* 257:1929–1933.
- Begun DR (1993) New catarrhine phalanges from Rudabanya (northeastern Hungary) and the problem of parallelism and convergence in the hominoid postcranial morphology. *J. Hum. Evol.* 24:373–402.
- Begun DR, and Kordos L (1997) Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene and living hominoids. In DR Begun, CV Ward, and MD Rose (eds): *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. New York: Plenum Press, pp. 291–316.
- Berggren WA, Kent DV, Flynn JJ, and Van Couvering JA (1985) Cenozoic geochronology. *Geol. Soc. Am. Bull.* 96:1407–1418.
- Birchette MG (1982) The Postcranial Skeleton of *Paracolobus chemeroni*. Ph.D. dissertation, Harvard University.
- Bown TM, Kraus MJ, Wing SL, Fleagle JG, Tiffney BH, Simons EL, and Vondra CF (1982) The Fayum Primate Forest revisited. *J. Hum. Evol.* 11:603–632.
- Bown TM, Fleagle JG, Kappelman J, Swisher CC, and Yirga S (1994) Age of Pliocene and Miocene primates from Fejej, Ethiopia (abstract). *Am. J. Phys. Anthropol.* 18:57–58.
- Cande SC, and Kent DV (1995) Revised calibration of the geomagnetic polarity time scale for the Late Cretaceous and Cenozoic. *J. Geophys. Res.* 100:6093–6095.
- Ciochon RL (1993) Evolution of the Cercopithecoid forelimb: Phylogenetic and functional implications from morphometric analyses. *Univ. Calif. Publ. Geol. Sci.* 138:1–251.
- Conroy GC (1976) Primate postcranial remains from the Oligocene of Egypt. *Contr. Primatol.* 8:1–123.
- Corruccini RS (1978) Morphometric analysis: Uses and abuses. *Yrbk. Phys. Anthropol.* 21:134–150.
- Darroch JN, and Mosimann JE (1985) Canonical and principal components of shape. *Biometrika* 72:241–252.

- Delson E, and Andrews P (1975) Evolution and interrelationships of the Catarrhine primates. In WP Luckett and FS Szalay (eds): *Phylogeny of the Primates*. New York: Plenum, pp. 405–446.
- Demes B, Stern JT, Hausman MR, Larson SG, McLeod KJ, Rubin CT (in press) Patterns of strain in the macaque ulna during functional activity. *Am. J. Phys. Anthropol.*
- Ehrensberg K (1938) *Austriacopithecus*, ein neuer menschen-affenartiger Primate aus dem Miozän von Kleinhadersdorf bei Poysdorf in Niederösterreich (Nieder-Donau). *S. Per. Akad. Wiss. Wies., Math-nat., abstr.* 147:71–100.
- Fisher RA (1953) Dispersion on a sphere. *Proc. Roy. Soc.* 217:295–305.
- Fleagle JG (1976) Locomotion and posture in the Malayan siamang and implications for hominoid evolution. *Folia primatol.* 26:245–269.
- Fleagle JG (1983) Locomotor adaptations of Oligocene and Miocene hominoids and their phyletic implications. In RS Corruccini and RL Ciochon (eds): *New Interpretations of Ape and Human Ancestry*. New York: Academic Press, pp. 301–324.
- Fleagle JG (1988) *Primate Adaptation and Evolution*. New York: Academic Press.
- Fleagle JG, and Kay RF (1987) The phyletic position of the Parapithecidae. *J. Hum. Evol.* 16:483–532.
- Fleagle JG, Simons EL, and Conroy GC (1975) Ape limb bone from the Oligocene of Egypt. *Science* 189:135–137.
- Fleagle JG, Stern JT, Jungers WL, Susman RL, Vangor AK, and Wells JP (1981) Climbing: A biomechanical link with brachiation and bipedalism. *Symp. Zool. Soc. Lond.* 48:359–373.
- Fleagle JG, Yirga S, Bown TM, Rasmussen DT, Assefa Z, Hagos T, and Negash A (1994) New paleontological discoveries from Fejej, southern Omo, Ethiopia. In Zewde B, Pankhurst R, and Beyene T (eds): *Proceedings of the Eleventh International Conference of Ethiopian Studies*. Addis Ababa: Addis Ababa University, pp. 15–22.
- Fleck RJ, Sutter JF, and Elliott DH (1977) Interpretation of discordant  $^{40}\text{Ar}/^{39}\text{Ar}$  age spectra of Mesozoic theoleiites from Antarctica. *Geochim. Cosmochim. Acta* 41:15–32.
- Grand TI (1972) A mechanical interpretation of terminal branch feeding. *J. Mammal.* 53:198–201.
- Harrison T (1986) A reassessment of the phylogenetic relationships of *Oreopithecus bambolii* Gervais. *J. Hum. Evol.* 15:541–583.
- Harrison T (1987) The phylogenetic relationships of the early catarrhine primates: A review of the current evidence. *J. Hum. Evol.* 16:41–80.
- Harrison T (1989) New postcranial remains of *Victoriapithecus* from the middle Miocene of Kenya. *J. Hum. Evol.* 18:3–54.
- Harrison T (1992) A reassessment of the taxonomic and phylogenetic affinities of the fossil catarrhines from Fort Teman, Kenya. *Primates* 33:501–522.
- Harrison T, and Rook L (1997) Enigmatic anthropoid or misunderstood ape? The phylogenetic status of *Oreopithecus bambolii* reconsidered. In DR Begun, CV Ward, and MD Rose (eds): *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. New York: Plenum Press, pp. 327–362.
- Hildebrand M (1995) *Analysis of Vertebrate Structure*. New York: John Wiley and Sons.
- Howell AB, and Straus WL Jr (1933) The muscular system. In CG Hartman and WL Straus Jr (eds.): *The Anatomy of the Rhesus Monkey*. New York: Hafner, pp. 89–175.
- Hürzeler J (1958) *Oreopithecus bambolii* Gervais: A preliminary report. *Verh. Naturf. Gesell. Basel* 69:1–48.
- Jenkins FA Jr (1973) The functional anatomy and evolution of the mammalian humero-ulnar articulation. *Am. J. Anat.* 137:281–298.
- Jenkins FA Jr (1981) Wrist rotation in primates: A critical adaptation for brachiators. *Symp. Zool. Soc. Lond.* 48:429–451.
- Jungers WL (1985) Body size and scaling of limb proportions in primates. In WL Jungers (ed): *Size and Scaling in Primate Biology*. New York: Plenum Press, pp. 345–381.
- Jungers WL (1987) Morphometric affinities of the appendicular skeleton of *Oreopithecus bambolii* (IGF 11778). *J. Hum. Evol.* 16:445–456.
- Jungers WL, Falsetti AB, and Wall CE (1995) Shape, relative size, and size-adjustments in morphometrics. *Yrbk. Phys. Anthropol.* 38:137–161.
- Kelley J (1995) A functional interpretive framework for the early hominoid postcranium (abstract). *Am. J. Phys. Anthropol.* 20:125.
- Kelley J, and Pilbeam DR (1986) The *Dryopithecines*: Taxonomy, comparative anatomy, and phylogeny of Miocene large hominoids. In DR Swindler and J Erwin (eds): *Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy*. New York: Alan R. Liss, pp. 361–411.
- Kirschvink JL (1980) The least-squares line and plane and the analysis of palaeomagnetic data. *Geophys. Jour. Royal Astro. Soc.* 62:699–718.
- Kitko R, and Richmond BG (1997) The functional and taxonomic affinities of KNM-FT3381 (abstract). *Am. J. Phys. Anthropol.* 24:144.
- Klecka WR (1980) *Discriminant Analysis*. Beverley Hills, CA: Sage Publications.
- Kretzoi M (1975) New ramapithecines and *Pliopithecus* from the lower Pliocene of Rudabanya in northeastern Hungary. *Nature* 257:578–581.
- Larson SG (1993) Phylogeny. In BF Monrey (ed): *The Elbow and Its Disorders*, 2nd Edition. Philadelphia: WB Saunders, pp. 6–15.
- Larson SG (in press) Parallel evolution in the hominoid trunk and forelimb. *Evol. Anthropol.*
- Leakey REF, and Leakey MG (1986) A new Miocene hominoid from Kenya. *Nature* 324:143–148.
- Leakey REF, and Walker AC (1985) New higher primates from the early Miocene of Buluk, Kenya. *Nature* 318:173–175.
- Leakey REF, Leakey MG, and Walker AC (1988) Morphology of *Turkanapithecus kalakolensis* from Kenya. *Am. J. Phys. Anthropol.* 76:277–288.
- LeGros Clark WE, and Thomas DP (1951) Associated jaws and limb bones of *Limnopithecus macinnesi*. *Fos. Mamm. Africa (BMNH)* 3:1–27.
- McCrossin ML, and Benefit BR (1992) Comparative assessment of the ischial morphology of *Victoriapithecus macinnesi*. *Am. J. Phys. Anthropol.* 87:277–290.
- McCrossin ML, and Benefit BR (1994) Maboko Island and the evolutionary history of Old World monkeys and apes. In RS Corruccini and RL Ciochon (eds): *Integrative Paths to the Past*. Englewood Cliffs, NJ: Prentice Hall, pp. 95–122.
- McCrossin ML, and Benefit BR (1997a) New postcranial remains of *Kenyapithecus* and their implications for understanding the origins of hominoid terrestriality (abstract). *Am. J. Phys. Anthropol.* 24:164.
- McCrossin ML, and Benefit BR (1997b) On the relationships and adaptations of *Kenyapithecus*, a large-bodied hominoid from the Middle Miocene of eastern Africa. In DR Begun, CV Ward, and MD Rose (eds): *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. New York: Plenum Press, pp. 241–267.
- McDougall I, and Watkins RT (1985) Age of hominoid-bearing sequence at Buluk, northern Kenya. *Nature* 318:175–178.

- McHenry HM, and Corruccini RS (1975) Distal humerus in hominoid evolution. *Folia Primatol.* 23:227–244.
- Morbeck ME (1975) *Dryopithecus africanus* forelimb. *J. Hum. Evol.* 4:39–46.
- Morbeck ME (1983) Miocene hominoid discoveries from Rudabanya: Implications from the postcranial skeleton. In RS Corruccini and RL Ciochon (eds): *New Interpretations of Ape and Human Ancestry*. New York: Academic Press, pp. 369–404.
- Mosimann JE (1970) Size allometry: Size and shape variables with characteristics of the lognormal and generalized gamma distributions. *J. Am. Stat. Assoc.* 66:930–945.
- Moya-Solà S, and Köhler M (1996) A *Dryopithecus* skeleton and the origins of great-ape locomotion. *Nature* 379:156–159.
- Napier JR, and Davis P (1959) The forelimb skeleton and associated remains of *Proconsul africanus*. *Foss. Mamm. Afr.* 16:1–70.
- O'Connor BL, and Rarey KE (1979) Normal amplitudes of pronation and supination in several genera of anthropoid primates. *Am. J. Phys. Anthropol.* 51:39–44.
- Oxnard CE (1963) Locomotor adaptations in the primate forelimb. *Symp. Zool. Soc. Lond.* 10:165–182.
- Oxnard CE (1972) Some African fossil foot bones: A note on the interpolation of fossils into a matrix of extant species. *Am. J. Phys. Anthropol.* 37:3–12.
- Oxnard CE (1975) Uniqueness and Diversity in Human Evolution: Morphometric Studies of Australopithecines. Chicago: University of Chicago Press.
- Prost JH (1965) A definitional system for the classification of primate locomotion. *Am. Anthropol.* 67:1198–1214.
- Richmond BG (1995) Diaphyseal curvature in living and fossil anthropoid humeri (abstract). *Am. J. Phys. Anthropol.* 20:181.
- Richmond BG, and Jungers WL (1995) Size variation and sexual dimorphism in *Australopithecus afarensis* and living hominoids. *J. Hum. Evol.* 29:229–245.
- Ripley S (1979) Environmental grain, niche diversification, and positional behavior in Neogene primates: An evolutionary hypothesis. In ME Morbeck, H Preuschoft, and N Gomberg (eds): *Environment, Behavior, and Morphology: Dynamic Interactions in Primates*. New York: Gustav Fisher, pp. 37–74.
- Rose MD (1983) Miocene hominoid postcranial morphology: Monkey-like, ape-like, neither, or both? In RL Ciochon and JG Fleagle (eds): *Primate Evolution and Human Origins*. New York: Aldine de Gruyter, pp. 189–193.
- Rose MD (1988) Another look at the anthropoid elbow. *J. Hum. Evol.* 17:193–224.
- Rose MD (1993) Locomotor anatomy of Miocene hominoids. In DL Gebo (ed): *Postcranial Adaptation in Nonhuman Primates*. DeKalb, IL: Northern Illinois University Press, pp. 252–272.
- Rose MD (1994) Quadrupedalism in some Miocene catarrhines. *J. Hum. Evol.* 26:387–411.
- Rose MD (1997) Functional and phylogenetic features of the forelimb in Miocene hominoids. In DR Begun, CV Ward, and MD Rose (eds): *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. New York: Plenum Press, pp. 79–100.
- Rose MD, Leakey MG, Lzakey REF, and Walker AC (1992) Postcranial specimens of *Simiolus enjiessi* and other primitive catarrhines from the early Miocene of Lake Turkana, Kenya. *J. Hum. Evol.* 22:171–237.
- Sarmiento EE (1985) Functional Differences in the Skeleton of Wild and Captive Orang-utans and their Adaptive Significance. PhD dissertation, New York University.
- Sarmiento EE (1987) The phyletic position of *Oreopithecus* and its significance in the origin of the Hominoidea. *Am. Mus. Nov.* 2881:1–44.
- Schmitt D (1994) Forelimb mechanics as a function of substrate type during quadrupedalism in two anthropoid primates. *J. Hum. Evol.* 26:441–457.
- Senut B (1989) Le coude des Primates Hominoïdes: Anatomie, fonction, taxonomie, évolution. *Cahiers de paléanthropologie*, CNRS.
- Simons EL (1960) *Apidium* and *Oreopithecus*. *Nature* 186:824–826.
- Simons EL (1994) New monkeys (*Prohylobates*) and an ape humerus from the Miocene Moghara Formation of Northern Egypt. *Proc. XIV Int. Primatol. Conf. Strasbourg, France*, 247–253.
- Simons EL (1995) Egyptian Oligocene primates: A review. *Yrbk. Phys. Anthropol.* 38:199–238.
- Steiger RH, and Jäger E (1977) Subcommission on geochronology: Convention in the use of decay constants in geo- and cosmochronology. *Earth Plant. Sci. Lett.* 36:359–361.
- Stern JT Jr (1971) Functional myology of the hip and thigh of cebid monkeys and its implications for the evolution of erect posture. *Biblio. Primat., No. 14*. Basel: Karger, pp. 1–318.
- Stern JT Jr, and Oxnard CE (1973) *Primate Locomotion: Some Links with Evolution and Morphology*. Basel: Karger. *Primatologia* 4.
- Strasser E (1988) Pedal evidence for the origin and diversification of cercopithecoïd clades. *J. Hum. Evol.* 16:81–99.
- Straus WL (1961) Primate taxonomy and *Oreopithecus*. *Science* 133:760–761.
- Suwa G, White T, Asfaw B, WoldeGabriel G, and Yemane T (1991) Miocene faunal remains from the Burji-Soyama area, Amaro Horst, Southern Sector of the Main Ethiopian Rift. *Palaeont. Afr.* 28:23–28.
- Swisher CC, Curtis GH, Jacob T, Getty AG, Suprijo A, and Widiasmoro BL (1994) Age of the earliest known hominids in Java, Indonesia. *Science* 263:1118–1121.
- Szalay FS, and Delson E (1979) *Evolutionary History of the Primates*. New York: Academic Press.
- Tiffney BH, Fleagle JG, and Bown TM (1994) Early to Middle Miocene angiosperm fruits and seeds from Fejej, Ethiopia. *Tert. Res.* 15:25–42.
- von Koenigswald GHR (1969) Miocene Cercopithecoidea and Oreopithecoidea from the Miocene of East Africa. In Leakey LSB (ed): *Fossil Vertebrates of Africa* (1). New York: Academic Press, pp. 39–52.
- Walker AC, and Pickford M (1983) New postcranial fossils of *Proconsul africanus* and *Proconsul nyanzae*. In RL Ciochon and RS Corruccini (eds): *New Interpretations of Ape and Human Ancestry*. New York: Plenum Press, pp. 325–351.
- Ward CV, Walker AC, and Teaford MF (1991) *Proconsul* did not have a tail. *J. Hum. Evol.* 21:215–221.
- Ward CV, Walker AC, Teaford MF, and Odhiambo I (1993) Partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. *Am. J. Phys. Anthropol.* 90:77–111.
- Watkins RT (1989) The Buluk Member, a fossil hominoid-bearing sedimentary sequence of Miocene age from northern Kenya. *J. Afr. Earth Sci.* 8:107–112.
- WoldeGabriel G, Yemane T, Suwa G, White T, and Asfaw B (1991) Age of volcanism and rifting in the Burji-Soyama area, Amaro Horst, southern Main Ethiopian Rift: Geo- and biochronologic data. *J. Afr. Earth Sci.* 13:437–447.
- Zapfe H (1958) The skeleton of *Pliopithecus* (*Epipliopithecus*) *vindobonensis* Zapfe and Hürzeler. *Am. J. Phys. Anthropol.* 16:441–458.